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TOMATO MOSAIC

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Fig. 1. Smooth ground cherry or Physalis, a very common Indiana weed which is a dangerous enemy of the tomato crop because it carries the destructive mosaic disease over winter. This weed lives over winter by a deep rootstock and after the weed becomes infected this rootstock sends up mosaic shoots year after year which serve as a source of early infection for tomatoes.

PURDUE UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

LAFAYETTE, INDIANA

TOMATO MOSAIC

The mosaic disease of tomatoes causes serious losses in yield in the greenhouse, market garden, and canning crops.

Mosaic is highly infectious and spreads with extreme rapidity.

The disease exhibits a variety of symptoms.

The same disease also affects tobacco, pepper, petunia, and a number of related plants including many weeds.

Mosaic is readily transmitted by inoculating a healthy plant with some of the juice of a mosaic plant.

The disease is spread largely by insects, especially plant lice, and by certain cultural operations, such as pruning and transplanting.

No indications of mosaic resistance have been noted in the numerous strains and varieties of tomatoes tested.

Diseased plants do not recover.

Mosaic does not persist in the soil or litter.

Mosaic is not transmitted through the seed.

Tomato mosaic is carried over winter by certain weeds which send up new shoots from deep rootstocks each spring.

In Indiana the disease occurs on four of these weeds, horse nettle and three species of ground cherry, and has been experimentally transmitted from each of these to tomatoes.

Two of these ground cherry species are extremely abundant and are the principal mosaic carriers.

A considerable percentage of the ground cherry shoots in old tomato fields have come up showing mosaic the next year and the second year after the tomatoes.

The disease may spread several hundred feet from these fields.

Practically no mosaic has been found among these weeds except in the vicinity of tomatoes, past or present.

Once introduced, mosaic will persist and spread year after year in the weeds. Since many new fields are used each year for tomatoes this reservoir of mosaic infection is increasing at an alarming rate.

Among numerous fields of tomatoes examined, mosaic occurred on the tomatoes in a high percentage of the fields that contained ground cherry mosaic.

A critical feature is the presence of ground cherries in and near plant-beds where they may serve as a source of early infection for the tomato plants.

Abundant evidence of the plant-bed origin of mosaic has been obtained. The disease is transported far and wide with the transplants.

Tobacco growers also should understand the importance of the weeds that harbor mosaic.

MOSAIC CONTROL SUGGESTIONS

1. Do not use tomato transplants from plant-beds in which mosaic is present. Guard against spread during transplanting.
2. Eradicate all horse nettles and ground cherries in and near greenhouses, plant-beds, and tomato fields early in the season.
3. Keep tomato fields free of all Solanaceous weeds, annual or perennial.
4. Keep plant-beds free of all weeds and tomatoes during the summer.
5. Keep greenhouses free of volunteer tobacco and tomato plants and all related weeds.
6. Control insect carriers by spraying or fumigation.

TOMATO MOSAIC

MAX W. GARDNER and JAMES B. KENDRICK [1]

Until recently no control for the mosaic disease of tomatoes was known, but it now seems evident that growers can without great difficulty do much to reduce the destructiveness of this disease, which annually causes losses in the greenhouse, market garden, and canning crops. As a result of investigations carried on in the Botanical Department of this Experiment Station during the last three years, it has been found that certain common weeds related to the tomato are sources of mosaic infection. Consequently the destruction of these weeds is essential in mosaic prevention.

The mosaic disease is highly infectious, spreads with extreme rapidity, and seems to be increasing in prevalence, especially in the canning crop. A number of crops such as cucumbers and beans are subject to similar mosaic diseases. The disease which affects tomatoes also occurs on tobacco and on the latter was one of the first mosaic diseases to be studied. It was called "mosaic" because its conspicuous symptom is the mottled appearance of the leaves suggestive of a mosaic pattern in dark and light green.

From the results of the study of tobacco mosaic and later of other mosaics, the outstanding characteristic of these troubles is known. This is the fact that, while no parasitic organisms such as bacteria have been found responsible for the diseased condition, it is readily transmissible from plant to plant by any means in which some of the juice of a diseased plant is introduced into the living tissues of a healthy plant.

It is our purpose herein to summarize what is known about tomato mosaic and to suggest methods of control based largely upon the weed relationship to the disease.

PREVIOUS INVESTIGATIONS

The disease as it occurs on tobacco was first described in Holland in 1886 and since then has been studied in Russia, France, Java, and the United States. Tobacco mosaic has been studied extensively by Clinton (9) in Connecticut, Allard (1, 2, 4) at Washington, who has given a good account of the earlier work, and Chapman (7) in Massachusetts. Allard (2, 4) demonstrated the importance of aphids or plant lice in the transmission of mosaic and proved that the disease does not persist in the soil.

Woods (21) at Washington in 1902 seems to have been the first to recognize tomato mosaic as a disease very similar to tobacco mosaic. He was able to transmit the disease by cutting back the plants, a phenomenon which was corroborated a few years later by a Dutch worker in Java. Clinton observed tomato mosaic under field conditions in 1907 and later (8, 9) secured by inoculation certain of the less common symptoms to which reference will again be made. In 1910, Miss Westerdijk (20) reported her studies of tomato mosaic in Holland in which she found the disease readily transmissible by inoculation but erroneously concluded that it was seed borne.

[1] The writers wish to acknowledge their indebtedness to Prof. H. S. Jackson for helpful suggestions and criticism.

Tomato mosaic has apparently caused trouble in greenhouses for many years but the symptoms and behavior have been so variable that the identity of the trouble frequently was not suspected. That a mosaic disease may exhibit a wide range of symptoms is well known as a result of recent intensive studies of the cucumber mosaic (11). Judging from the various mosaic symptoms that others have recognized on tomatoes and that have resulted from our own inoculation tests, it seems very likely that many of the puzzling greenhouse tomato diseases or winter blights reported in literature were merely different manifestations of mosaic.

The disease described and illustrated by Bailey (5) at Cornell University in 1892 as winter blight of greenhouse tomatoes very closely resembles mosaic in its more destructive form. Bailey observed that it reduced the yield, that it spread from plant to plant, and that it was not a soil trouble. The blight of greenhouse tomatoes reported from Ohio by Selby (19) in 1896 was very likely the same disease. Similar diseases of uncertain character have also been reported from Pennsylvania and Ontario.

Osner in unpublished inoculation and filtration tests carried out at this experiment station proved that the common disease in Indiana greenhouses which closely resembled the so-called winter blight was mosaic in character and consequently in all probability identical with typical mosaic. Mosaic in its more typical form has been reported in greenhouses and described at some length by Chapman in Massachusetts in 1908 and again in 1913 (6) and pathologists in Maryland, Ohio, and Oregon have found the disease destructive on greenhouse tomatoes. Mosaic showing typical symptoms has also been common in Indiana greenhouses for many years.

It is evident therefore that tomato mosaic seems to have been noted in the past largely in greenhouses. Until rather recently not much attention has been devoted to the disease in the field crop. It has, however, been reported as a serious field disease in Australia and Ontario and in New Jersey and many other states in this country, particularly in the canning crop. It is as a field disease that mosaic has become a serious factor in the Indiana tomato industry.

GEOGRAPHICAL DISTRIBUTION OF MOSAIC

The mosaic disease on tobacco is worldwide in its distribution and the disease on tomatoes has been recorded from Europe, Australia, Ontario and in the United States, according to the federal plant disease survey, from twenty-three states including such important tomato regions as the New Jersey, Maryland, and Delaware area, Florida, Louisiana, and California. The occurrence of the disease in Georgia as well as Louisiana should be of interest to northern growers who use southern-grown plants.

In Indiana, tomato mosaic has been found during the last three years in the following counties: Lake, Tippecanoe, Clinton, Howard, Grant, Tipton, Marion, Hancock, Johnson, Vigo, Sullivan, Knox, Orange, and Washington. In the canning crop the disease seems to be more prevalent in the central than in the southern part of the state.

Fig. 2. Leaf symptoms of mosaic on tomato.
A. Leaf from a mosaic plant showing dwarfing and distortion of leaflets.
B. Leaf from a healthy plant.

MOSAIC CAUSES LOSS IN YIELD

Many observers have noticed that mosaic is most severe in its effects upon rapidly growing plants and upon the young developing organs. Possibly this explains its greater severity under greenhouse conditions. It is a matter of common observation that many plants that are infected early in the season may show very extreme effects of mosaic and bear no marketable fruit whatever. Others may bear a greatly reduced yield, while, in the case of plants infected late in the season, the effect on the yield is not very noticeable.

Although many have noted this reduction of yield by mosaic, there is very little exact data bearing upon this point. Norton (18) found that in the greenhouse 33 per cent less fruit was set on diseased than on healthy plants. McCubbin (15) reports studies of the loss due to mosaic under field conditions in Ontario as shown in table I.

TABLE I.—Effect of Mosaic on Yield

	Number of fruits	Weight of fruits
59 healthy plants	7,135	819.5 pounds
59 mosaic plants	4,740	599.0 pounds
Percentage loss due to mosaic	36.8 per cent	40.5 per cent

In the 1919 report of the federal plant disease survey, heavy losses due to mosaic are reported for Florida, California, and Pennsylvania, and in the 1920 report, the total loss due to mosaic was recorded as 5 to 10 per cent of the total crop for Louisiana, 9 per cent for Iowa, and 7 per cent for California. Under Indiana conditions it has become evident that mosaic is a serious factor in the canning crop owing to the fact that the disease secures an early start and that by the end of summer the percentage of infection in most fields is very high.

Fig. 3. Typical mosaic symptoms on tomato leaflets. Note the distortion and malformation of the leaflets, and the raised dark green spots on a lighter green or yellowish background.

Furthermore, mosaic causes losses in other ways. Occasionally plants are killed outright. This has been noted in greenhouses and among infected transplants set out in very poor field soil. In addition, mosaic frequently produces a severe blemish of the fruit in the form of dry, brown streaks, blotches, and spots of varying size and shape (Fig. 6). This effect has been recorded under greenhouse conditions by many investigators and has been noted in abundance in California tomatoes received on the Chicago market. By heavy artificial inoculation in midsummer similar fruit effects have been produced in a number of varieties under field conditions (Fig. 5).

TOMATO MOSAIC AFFECTS RELATED PLANTS

So far as is known at present, this disease is confined to plants related to the tomato, that is, members of the family Solanaceae (2, 9). This includes tobacco, peppers, petunia, and a number of weeds to which reference will be made later. The disease on tobacco and peppers is of common occurrence in Indiana. Potatoes also belong to the same family of plants and are subject to a prevalent and destructive mosaic disease which likewise occurs commonly in Indiana but the relation of potato mosaic to the disease under consideration has not yet been settled. Melhus (16) has recently reported evidence that these diseases are identical and in preliminary cross inoculation tests we have obtained similar evidence. Melhus (16) also reports that the eggplant is susceptible to mosaic.

In extensive field tests with a large number of tomato varieties, all have proved susceptible to mosaic. By artificial inoculation we have transmitted the disease to the currant tomato (*Lycopersicum pimpinnellifolium*), the cherry tomato (*L. esculentum*, var. *cerasiforme*), and the Chinese scarlet eggplant (*Solanum integrifolium*) and have observed mosaic on the husk tomato (Physalis sp.).

Fig. 4. Less typical mosaic symptoms produced by inoculation of tomato plants in the field.
A. Mosaic leaf of Chalk's Early Jewel variety showing fine crinkling and curling or rolling of the leaflets. A bronzed discoloration may accompany such symptoms.
B. Brown, dead spots and streaks on stem of Peerless variety, accompanied by blighting of leaves.

MOSAIC SYMPTOMS CONSPICUOUS

Tomato mosaic may exhibit such a variety of symptoms and effects that any description must be more or less inadequate. This situation has resulted in confusion in the literature and perhaps frequent failure to recognize the disease in its various manifestations. Temperature, rate of growth, and age of plant are factors which greatly influence the expression of mosaic symptoms. As a rule the symptoms appear only on the parts of the plant that are in a growing condition at the time of infection or that

develop after that time. Usually all growing points of a plant show the symptoms although exceptions to this have been noted in Indiana and elsewhere. Infected plants practically never recover, although the symptoms may become less conspicuous as the plants grow older or when cooler temperatures prevail.

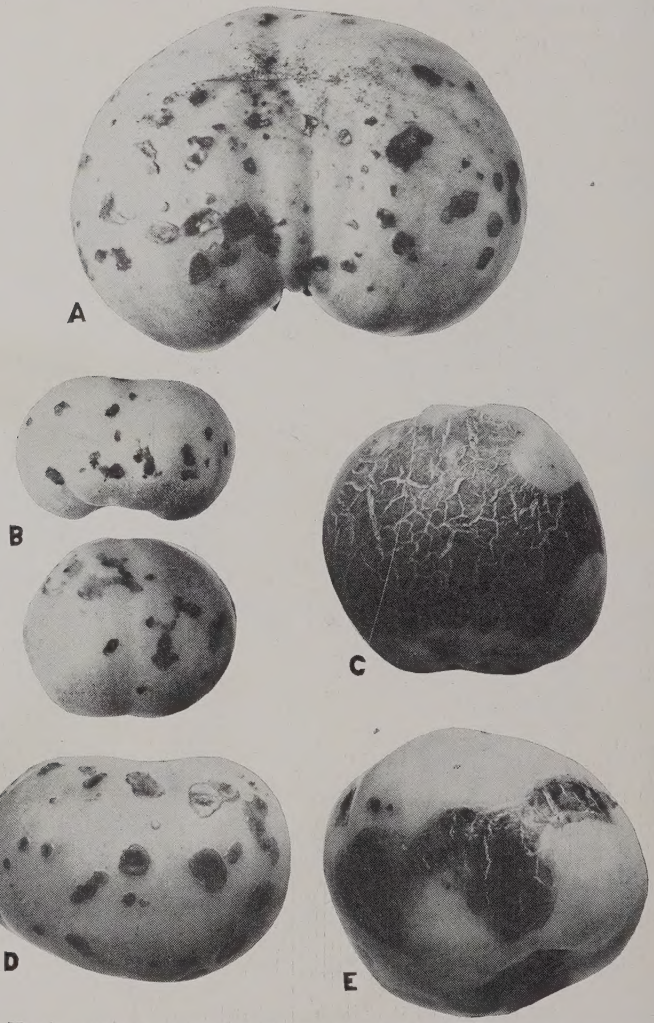

Fig. 5. Mosaic symptoms on tomatoes produced by field inoculations made Aug. 3, 1921.

A. Irregular raised brown spots on Earliana variety.
B. Sunken brown spots, Livingston's Beauty variety.
C. Large blotch, sunken, cracked.
D. Raised greasy spots on Matchless variety.
E. Mosaic blotch with cracks appearing.

The most characteristic symptom of mosaic is the mottling of the younger leaflets due to the appearance of lighter green or yellowish areas of various shapes and sizes (Fig. 9). The darker green portions are frequently raised or puffed up (Fig. 3). These effects are frequently accompanied by extreme stunting and malformation of the leaflets (Fig. 2). The leaflets may be distorted and crumpled or reduced to narrow ribbons. Severely diseased plants may be greatly stunted and bushy with a yellowish cast and the leaves so reduced as to warrant the term, "fern leaf." Such plants bear only stunted fruits or none at all.

Under greenhouse conditions and in case of heavy inoculation of rapidly growing plants in the field, the leaflets may become thickly spotted with small dead brown areas and curled downward about the margin. In other cases the leaflets may become curled, finely crinkled (Fig. 4A), and bronzed, or may show areas of yellowish mottled or speckled tissue (noted on Matchless variety) or wedges of yellowish or dead tissue extending inward from the margin (Fig. 7B). Young shoots may be blighted outright (Fig. 7A). Brown, dead spots and streaks occur on the petioles and stems (Fig. 4B) and elevated, greasy areas of irregular size and pattern appear on the green fruits (Fig. 5). These spots or streaks on the fruit soon become more or less dry, brown and sunken (Figs. 5B and 6) and the larger lesions show numerous shallow cracks as a result of the growth pressure of the fruit (Fig. 5, C and E). Such lesions are superficial but constitute very objectionable blemishes. Fruit lesions such as these occurred on certain plants among 18 out of 57 seedsmen's varieties inoculated in the field in midsummer (Aug. 3, 1921) and were almost always associated with the tip and leaf blight effect of the disease (Figs. 4B and 7A).

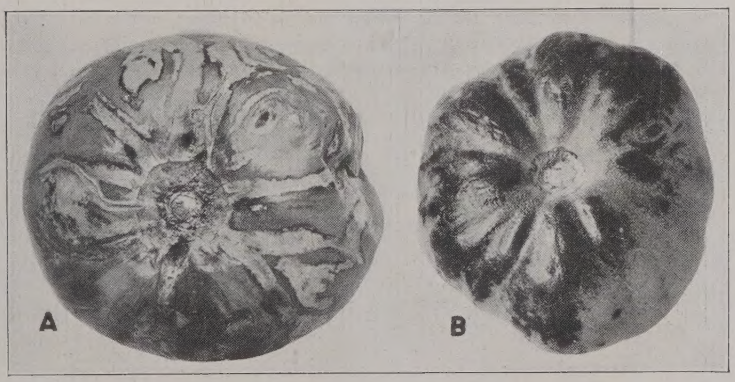

Fig. 6. Mosaic blemishes on tomatoes.

A. Irregular pattern of light, sunken stripes.
B. Brown blotching of stem end.

While this latter class of symptoms has not been as commonly recognized as the more typical symptoms first described, many workers have noted these severe effects, especially under greenhouse conditions.

MOSAIC CAUSED BY A "VIRUS"

The extreme infectiousness of mosaic has been mentioned as well as the fact that no organisms such as fungi or bacteria have been found responsible for the disease. The work of Allard (2, 4) on tobacco mosaic and of Doolittle (11) on cucumber mosaic has furnished important information concerning the nature of the cause of the mosaic diseases. The juice from a mosaic plant retains its power to produce the disease after passage through bacteria-proof porcelain filters and thus may be called a "filterable virus," a term previously used by medical men to characterize the causal factor in such diseases as rabies and infantile paralysis.

The tobacco and tomato mosaic virus seems to be distributed throughout all parts of a mosaic plant (2, 4). Inoculation is more successful in young growing tissues and the virus must be rubbed or inserted into the living tissues. A slight wound is necessary. Mosaic symptoms usually appear between one and two weeks after inoculation. Johnson (14) has recently shown that temperature has a marked effect upon this incubation period in the case of tobacco mosaic and that the symptoms appear most promptly between 82° and 86° F. The viruses of the different mosaic diseases are separate and distinct and are specific in their host preferences. For example, the virus of bean mosaic will not attack tomatoes and the converse is true.

Many properties of the tobacco mosaic virus have been determined. Allard found that it retained its infectivity even in dilutions of 1 to 1,000, that it survived drying, that it is precipitated by alcohol, and that it is killed by formaldehyde and by heating. Doolittle (11) has determined many of the properties of the cucumber mosaic virus and (11, p. 27) has presented a summarized comparison of these two viruses.

It has been a much debated question as to whether the activity of this virus is due to exceedingly small organisms invisible under the microscope and small enough to pass through the filters or to very active but lifeless chemical compounds such as enzymes. The extremely rapid increase of the causal principle within an inoculated plant argues in favor of the organism theory.

MOSAIC SPREAD BY CULTURAL OPERATIONS

Mosaic may be readily spread by any process which involves handling and wounding of the plants. It has long been known that in tobacco the disease is spread during the process of removing worms and cutting off the tops. It is evident that the knife, after cutting a diseased plant, may carry the virus to several healthy plants. The pruning of greenhouse and market garden tomatoes is a common means of spreading mosaic infection. Woods (21) and many others transmitted tomato mosaic in this way. Artificial pollination of greenhouse tomatoes is not likely to transmit the disease unless wounds are made. There is no evidence that the disease is transmitted in the pollen.

Fig. 7. A. Blighting of the growing tip of Success variety of tomato as a result of field inoculation, Aug. 3, 1921.

B. Brown wedge with yellow border in mosaic tomato leaflet.

Undoubtedly one of the most important means by which mosaic is spread in the canning crop is the handling of the plants during transplanting. Clinton (9) and Chapman (7) have shown that this occurs to a very considerable extent in the case of tobacco mosaic. If there are a few mosaic plants in the tomato plant-bed a workman may inoculate many healthy plants with the juice from diseased plants, through the very slight wounds made in pulling and replanting the plants. Allard (4) has shown that merely breaking off the hairs or trichomes on a tobacco leaf will afford wounds adequate to permit mosaic infection. Tomato plants are densely covered with these fragile, easily broken glandular hairs and trichomes and during the process of transplanting many of these hairs are rubbed or broken off, thus affording plenty of opportunity for entrance of the mosaic virus from the workman's hands. Clinton (9) and Allard (4) have found that thorough washing of the hands with soap and water will remove the virus.

Without doubt mosaic is spread very generally throughout tomato fields as soon as picking begins because of the handling and wounding of the plants, but much of this infection comes too late in the season to cause much loss.

MOSAIC SPREAD BY INSECTS

Allard's work (2, 4) with tobacco showed, however, that plant lice or aphids were the most important agency in the transmission of mosaic. Others have found the same true for cucumber mosaic and spinach mosaic. After feeding on a mosaic plant, an aphid becomes a carrier of the mosaic virus and may cause infection when it punctures the tissues of a healthy plant. No special investigation of the mode of transmission of tomato mosaic has been made. Aphids are abundant on tomatoes and plants grown under insect-proof cages (Fig. 8) remain free from infection so it seems safe to assume that aphids spread the disease. Some evidence against aphids and also flea-beetles is presented later.

Fig. 8. Tomato plants grown under these insect-proof cloth cages remain free from mosaic, even in a badly diseased field.

MOSAIC RESISTANCE HAS NOT BEEN FOUND

No varieties nor strains of the cultivated tomato have been found to be resistant to mosaic and in experimental fields the disease has been observed on a total of 63 seedsmen's varieties including most of the common garden and canning types and such varieties as Yellow Cherry, Red Cherry, Red Pear-shaped, Yellow Pear-shaped, and Yellow Plum.

In a large field containing a number of single plant strains of the Greater Baltimore variety in 1919, three strains seemed to show less mosaic than the others. Every alternate plant in these three rows was inoculated and three plants failed to develop mosaic symptoms. Seed was saved from these plants and grown the next year, but artificial inoculation was successful on all of the progeny and it was evident that no mosaic resistance had been inherited.

MOSAIC DOES NOT PERSIST IN SOIL

In combating any plant disease it is highly important to know how the parasite which causes the disease passes the winter and just how the

disease gets started in the spring. It has been shown for tobacco mosaic (2), and also for other mosaic diseases (11), that the trouble does not persist in the soil over winter nor in the litter from diseased plants and that infection does not proceed from the soil. There is no evidence that tomato mosaic differs in this respect from the disease as it occurs in tobacco.

TOMATO MOSAIC NOT SEED TRANSMITTED

While potato mosaic is transmitted through the seed tubers and bean mosaic and soybean mosaic are carried in the seed, seed transmission does not occur in tobacco and tomato mosaic and consequently it has until recently been unknown how this disease originated in the spring.

Miss Westerdijk (20) concluded upon the basis of very inadequate evidence that tomato mosaic was seed borne, but Allard (3) in well controlled and more extensive tests involving about a thousand tomato plants obtained no evidence of seed transmission. Nor was he able to secure any seed transmission in the case of tobacco mosaic although he had detected the virus in the ovary and ovules of the flower.

The annual recurrence of mosaic throughout the Indiana canning crop and especially in the seed-producing fields made it highly important to dispel all doubt as to whether or not the disease might be seed borne. Seed from individual mosaic tomato plants was saved in 1919 and 1920 and in addition a considerable quantity of seed was saved from mosaic plants in cooperation with I. C. Hoffman and H. D. Brown of the Department of Horticulture. This seed was grown under carefully controlled conditions in the greenhouse during the winter and spring of 1921 and in the greenhouse as well as under cloth cages in the field during the summer and in the total of 22,944 tomato plants grown from this seed no mosaic occurred and no evidence of seed transmission was obtained.

The possibility of the presence of the virus dried on the exterior of the seed coat was taken into consideration, but inoculation with the wash water from seed from mosaic plants yielded no infection whatever.

In the light of all the available evidence, there appears to be no indication whatever that tomato mosaic is transmitted through the seed. Consequently the mode of overwintering and source of early infection must be sought elsewhere.

GREENHOUSE TOMATOES MAY HARBOR MOSAIC

From the standpoint of the field crop it is necessary to recognize that the hothouse tomatoes may be the means of carrying the mosaic disease through the winter. Mosaic is of common occurrence in greenhouses and may readily be carried from them to the field crop in the spring either by insects or by means of the transplants which are often grown in the greenhouses or adjacent cold frames, later to be set out in the field. In one case noted in June, 1921, at Kokomo, a severe early infestation of mosaic was present in a field the plants for which had been grown in a hothouse occupied by a tomato crop. In fact mosaic was found among the transplants left in the greenhouse bench.

However, hothouse tomatoes are grown in relatively few localities in the state and are usually near towns. Market gardens might be thus en-

dangered but the canning crop is contracted primarily among general farmers so that the fields are widely scattered and as a rule are not in the neighborhood of hothouses. Therefore greenhouses can play only a very minor role as reservoirs of mosaic infection for the canning tomato crop.

Right in this connection it is important to note that if it should be proved that potato mosaic is identical with tomato mosaic, mosaic potatoes must be considered a menace to tomato crops in the immediate vicinity.

WEEDS SUBJECT TO TOMATO MOSAIC

Allard (2) transmitted mosaic from tobacco to the annual weeds, nightshade (*Solanum nigrum*) and Jimson weed (*Datura stramonium*), and to horse nettle (*Solanum carolinense*) which is perennial by means of a deep rootstock. Clinton (9) transmitted the disease to a species of ground cherry (Physalis). Harper found mosaic on the perennial apple of Sodom (*Solanum aculeatissimum*) in Florida and Nishimura (17) transmitted the disease from this weed to tobacco. Crawford (10) in Iowa found a perennial species of ground cherry (*Physalis longifolia*) subject to the mosaic disease.

Fig. 9. Conspicuous mosaic symptoms on black nightshade, a common annual weed. A. Healthy leaf. B. Two mosaic leaves.

In Indiana we have found mosaic occurring naturally on the annuals, nightshade (Fig. 9) and Jimson weed, and on annual species of ground cherry (Physalis). We have been unable to prove that the disease on Jimson weed crosses to tomatoes although both diseases have been found in the same field, and we have been unable to infect buffalo bur (*Solanum rostratum*) with tomato mosaic. However, our greatest concern is with the perennial weeds or those which overwinter by means of a root or rootstock.

PERENNIAL GROUND CHERRIES AND HORSE NETTLE HARBOR MOSAIC

The occurrence of mosaic in perennial weeds is of extreme significance. Allard (2) pointed out the danger of the disease overwintering in horse nettle and Crawford (10) has recently proved that the disease is carried overwinter in the rootstocks of the ground cherry species, *Physalis longifolia*, in tests carried out simultaneously with our own studies (13) in Indiana.

The following perennial weed relatives of the tomato occur in Indiana[1]:

Matrimony vine (*Lycium halimifolium*)
Bittersweet (*Solanum dulcamara*)
Prairie ground cherry (*Physalis lanceolata*)
Horse nettle (*Solanum carolinense*) (Fig. 13).
Clammy ground cherry (*Physalis heterophylla*) (Fig. 12)
Smooth ground cherry (*Physalis subglabrata*) (Figs. 1 and 10)
Virginia ground cherry (*Physalis virginiana*)

The first three weeds in the above list have not been found common in the tomato regions and with the exception of a successful inoculation of bittersweet with tomato mosaic no evidence against these weeds has been obtained. However, they should be considered undesirable near tomatoes.

We have found mosaic occurring naturally on the last four weeds in the list and have successfully transmitted the disease from each of these to tomatoes. These four weeds are of common occurrence in cultivated fields in Indiana and all are perennial by means of a deep rootstock which sends up new shoots every year. The rootstocks are too deep to be destroyed by ordinary cultivation practices and hence these weeds are very difficult to eradicate.

The mosaic symptoms are conspicuous on these weeds during the spring and early summer (Figs. 11 and 12B), but later in the season may be very inconspicuous. In the case of horse nettle, Allard (2) has pointed out that the symptoms may be lacking although the virus is present and Nishimura (17) noted the same condition in *Physalis alkekengi*.

In the canning tomato regions of central Indiana, the smooth and the Virginia ground cherry (Figs. 1 and 10) are by far the most abundant of the weeds listed. Most of the subsequent data refers to these two species which are so nearly alike in appearance that in our survey work no effort has been made to differentiate them and, unless otherwise qualified, the terms, Physalis, or ground cherry, as used herein should be understood to refer to these two very similar species.

Once these weeds become infected with mosaic, the rootstocks send up mosaic shoots the next year and from these the disease may spread to tomatoes. This was proved conclusively by digging the rootstocks of mosaic plants of smooth ground cherry in August, 1920, and planting them in a small plot surrounded by a wooden frame sunk in the soil in an

[1] Mr. Charles C. Deam, state forester, very kindly furnished authoritative records relative to the Solanaceous weed flora of Indiana.

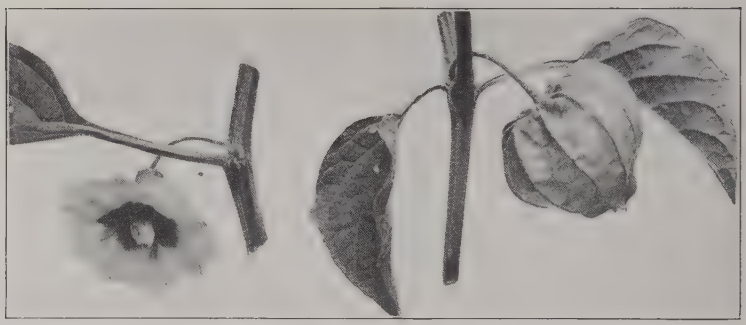

Fig. 10. Leaf, flower and fruit of smooth ground cherry or Physalis, one of the weeds which carries the mosaic over winter. Virginia ground cherry is very similar.

experimental garden near the station. In the spring of 1921 these root-stocks sent up shoots showing mosaic. Six shoots had appeared by May 13, thirteen by May 23, and on June 3, fifteen plants were present. The mosaic shoots were up well before the date that tomatoes are transplanted to the field. All showed definite mosaic symptoms as soon as the leaves unfolded and the disease was transmitted from these to potted tomato plants in the greenhouse by artificial inoculation and also by transferring plant lice.

MOSAIC GROUND CHERRY IN OLD TOMATO FIELDS

The occurrence of mosaic on Physalis or ground cherry was first noted in the summer of 1919 in an experimental tomato field near Frankfort. Mosaic was also prevalent on the tomatoes and reciprocal cross inoculations between tomatoes and ground cherry were successful. In a general survey of the neighborhood no mosaic was noted on the weeds at any distance from this field.

In 1920 no tomatoes were grown near this field but mosaic occurred very generally on the ground cherries throughout the field and to a much greater extent than had been noted in 1919.

On May 24, 1921, another examination was made of the ground cherries in this field which had been in tomatoes two years before, and mosaic was again found very prevalent. Out of 203 of the weeds examined, 147 or 74 per cent showed mosaic. Along the edges of adjacent fields, a few mosaic weeds were also found. Thus the disease had persisted two years in the weeds in this field and had even spread and become more prevalent.

On May 23, 1921, mosaic ground cherries were found in a small plot and in a field near LaFayette in both of which tomato mosaic had occurred in 1920.

On May 25, 1921, an examination was made of a small field near Indianapolis in which tomato mosaic had been especially severe in 1920. Out of 368 ground cherry plants noted, 73 or 20 per cent were mosaic. No mosaic had been noted among these weeds the preceding September but this may be attributed to the fact that towards the end of the season

mosaic symptoms on the weeds as well as the tomatoes may become indistinguishable.

These observations showed that mosaic ground cherry shoots were appearing rather generally in fields which had been in tomatoes in previous years, well before the date when the tomato plants for the current season would be transplanted to the field. It is evident that the ground cherries once infected constitute a perennial reservoir of mosaic infection which increases annually and which remains a constant danger to any future crops of tomatoes (or tobacco) in the vicinity.

Further observations were made later in the season upon the prevalence of mosaic among the ground cherries in fields previously in tomatoes. In the field near LaFayette in which tomato mosaic had occurred the previous year, 43 out of 77 or 55 per cent of the ground cherries examined the third week in July showed mosaic. A number of volunteer tomato plants had come up in this field but no mosaic was found among the 186 examined although later in the season a few developed the disease.

A study of the mosaic prevalence among the ground cherries was made July 13, 1921, on a large farm near Indianapolis of which a considerable acreage was devoted to tomatoes in 1918, 1919, 1920 and 1921. The 1919 crop, comprising about 100 acres, was practically 100 per cent mosaic in September of that year and some mosaic on ground cherry was noted at that time. The results of the survey of eight fields on this farm and the relation between previous tomato crops and ground cherry mosaic are presented in table II.

TABLE II.—Ground Cherry Mosaic in Old Tomato Fields

Field	Crop			Ground cherry plants, July 13, 1921		
	1919	1920	1921	Number examined	Number Mosaic	Per cent Mosaic
1	Tomatoes	Corn	Corn	79	43	54
2	Tomatoes	Oats	Clover	34	7	20
3	Tomatoes	Corn	Oats	61	16	26
4		Tomatoes	Oats	27	17	63
5		Tomatoes	Weeds	40	27	67
6		Tomatoes	Wheat	107	55	51
7	Not tomatoes		Tomatoes	138	34	25
8	Not tomatoes		Wheat	543	4	0.7

The figures in table II show how prevalent mosaic may be among these weeds one and two years after tomatoes have been grown. The scarcity of the disease in field 8 which had never been in tomatoes indicates that the high incidence of mosaic in fields 1 to 6 was due to the previous tomato crops.

Surveys of numerous wheat stubble and corn fields has revealed that mosaic very rarely occurs on the ground cherries except in the vicinity of tomato crops, past or present. In only two instances have apparently spontaneous cases of mosaic on the weeds been found and each of these consisted of a single infected plant. Thus it is unsafe to conclude that

Fig. 11. Mosaic symptoms on leaves of smooth ground cherry or Physalis. A. Two healthy leaves. B. Six mosaic leaves.

mosaic was originally present in these weeds, but it is evident that once introduced by means of tomatoes, the disease will persist indefinitely in the weed hosts.

Under Indiana conditions, canning tomatoes are grown in rotation with other crops and many new fields are used each year for tomatoes. Thus the mosaic disease will undoubtedly be introduced into the weed population of new fields and localities each season where it will persist indefinitely. This will inevitably result in an alarming annual increase in the reservoir of mosaic infection for future tomato crops unless the vicious cycle is broken. The accumulation of cucumber mosaic infection in the perennial milkweeds which have recently been incriminated by Doolittle and Walker (12) has driven the pickle industry out of one territory after another and tomato growers should recognize the analogy in the weed relation to tomato mosaic.

DISTANCE MOSAIC MAY BE SPREAD

The occurrence of mosaic on ground cherries along the edges of fields adjacent to the Frankfort tomato field has been mentioned. An exceptional record was the presence of two mosaic plants at a distance of 40 rods from this field.

Field 8 in table II had never been in tomatoes and the nearest tomato crop, that of 1919 in field 1, was 400 feet distant. The few cases of mosaic

ground cherry in field 8 were found along the edge nearest to the former tomato field and are probably attributable to long distance spread from that field.

In another wheat stubble field which had never been in tomatoes, mosaic was found on ground cherries along the edge adjacent to one of the 1919 tomato fields (field 3, table II) in a strip 150 to 250 feet wide but no mosaic was noted at greater distances from the edge of the field. Thus it is evident that the disease may be carried several hundred feet among the weeds.

Long distance dissemination of mosaic is effected by the transport of infected tomato transplants from one region to another. For example, the mosaic noted in certain fields in Hancock county, July 20, 1921, had been brought in with transplants grown 20 miles away. Further reference to this phase of the problem will be made in the discussion of the plant-bed origin of mosaic.

INSECTS CARRY MOSAIC BETWEEN WEEDS AND TOMATOES

Insects probably carry the disease from the tomatoes to the weeds and from the weeds to the tomatoes. Plant lice were noted on mosaic ground cherry shoots May 23, 1921, and about 25 of these insects were collected and caged over three small healthy tomato plants in the greenhouse. Two weeks later one of these tomato plants showed mosaic, while none of the six plants held as controls developed the disease. The plant lice soon disappeared from the weeds but their presence early in the season is significant.

The small black flea-beetles are abundant on ground cherries as well as horse nettle throughout the season and these beetles also attack young tomato plants. A preliminary test indicates that these insects may carry mosaic. On July 16, 1921, a number of flea-beetles collected on mosaic ground cherries were placed in a large cloth cage covering young healthy tomato plants. On August 17, six of the 338 plants in this cage showed mosaic while none was found among the 218 control plants in a similar cage in which no flea-beetles had been placed.

Thus plant lice and flea-beetles are possible carriers since they feed on both the weeds and the tomatoes and observational evidence would indicate that much of the transference of the disease between the weeds and the tomatoes might occur very early in the season.

GROUND CHERRY AND MOSAIC IN TOMATO FIELDS

To ascertain the general prevalence of ground cherry and of mosaic infection in the ground cherry in Indiana tomato fields and the possible correlation between these factors and mosaic in the tomato crop, a number of canning crop fields in six localities were examined in the season of 1921. Of necessity much of this survey was hastily performed. There are included in this survey two fields in Washington county visited June 20; 13 fields in Johnson county, June 30; 21 fields in Howard and Tipton counties, July 2; four fields near Southport, July 13; 11 fields in Hancock county, July 20; 25 fields in Marion county, July 21; and five fields in Grant county, Sept. 17. The results may be summarized as follows:

Tomato fields examined	81
Fields in which ground cherry was found	65
Fields in which mosaic on ground cherry was found	35
Fields in which mosaic on tomatoes was found	60
Fields in which ground cherry and mosaic on tomatoes were found	48
Fields in which mosaic on both ground cherry and tomatoes was found	29

The wide occurrence of ground cherry is evidenced by its presence in 65 out of 81, or 80 per cent, of the tomato fields examined. The prevalence of mosaic on ground cherry is shown by its presence in 35 out of 65, or 54 per cent, of the fields in which the weeds were noted, and in 43 per cent of all fields noted.

The prevalence of mosaic on tomatoes is indicated by its occurrence in 60 out of 81, or 74 per cent, of the fields examined.

A correlation between mosaic on tomatoes and the presence of ground cherries is indicated by the fact that 48 out of 65, or 74 per cent, of the fields containing ground cherry showed mosaic on the tomatoes and the fact that 48 out of 60, or 80 per cent, of the fields showing mosaic on tomatoes contained ground cherry plants.

Some degree of correlation between the occurrence of mosaic on both ground cherry and tomatoes is indicated by the presence of mosaic on tomatoes in 29 out of 35, or 83 per cent, of the fields in which it was found on ground cherry, and by the presence of mosaic ground cherry plants in 29 out of 60, or 48 per cent, of the fields in which mosaic was found on the tomatoes.

PLANT-BED ORIGIN OF MOSAIC

If, according to the theory advanced, the wholesale infection of the weeds in the fields proceeds from the tomato crop, what was the source of infection for the tomatoes?

Chapman (7) has found that a considerable proportion of the field outbreaks of tobacco mosaic can be traced to the seedbed, particularly old seedbeds. There was convincing evidence in many of the tomato fields examined in the course of the survey described above that mosaic was introduced into the field with the transplants. The instance of a field outbreak of mosaic originating in a greenhouse plant-bed near Kokomo has been referred to. In many of the tomato fields noted in Johnson and Hancock counties, mosaic was distinctly more prevalent on the transplants from certain sources. Previous mention has been made of the general occurrence of the disease in certain fields on the transplants secured from a grower in a town 20 miles away. An examination of the outdoor plant-beds from which these plants were obtained showed the disease very prevalent among the remnant tomato plants. These plant-beds were grown up to weeds and about 30 ground cherry plants were found, none of which, however, showed mosaic. In fact this weed was very abundant throughout this neighborhood. In other localities ground cherries were also found in or near tomato plant-beds.

Fig. 12. Clammy ground cherry, a common perennial weed which carries mosaic over winter.

A. Healthy plant and flower and fruit characters.
B. A leaf from a mosaic plant.

The critical feature of the tomato mosaic situation at present is considered to be the presence of ground cherry plants in and about plant-beds because tomato plants are grown here year after year and, once mosaic becomes established in these perennial weeds, all succeeding crops of tomato plants will be exposed to infection before they are transplanted to the field. This source of infection is especially dangerous because from one plant-bed the disease may be introduced into numerous fields and because early mosaic infection results in more serious reduction in yield. Furthermore, as has been pointed out, the disease may be transmitted from one diseased plant to many healthy plants by the handling of the plants involved in the process of transplanting. Each infected plant set out in a field serves as a center of infection for the rest of that crop and for the weed carriers as well.

It is by prevention of plant-bed infection by weed eradication that growers can most efficiently and most feasibly reduce mosaic losses.

The original infection of the weeds around plant-beds probably occurs in some previous season and is undoubtedly facilitated by the fact that gardens and tomato fields are often located near these plant-beds. From near-by fields and gardens, insects may carry mosaic to the weeds in and near the plant-bed, or to remnant tomato plants which are frequently allowed to grow in the plant-beds, and then from these to the weeds.

As to where mosaic came from in the first place, it is not our province to speculate. It is probably introduced into new regions with diseased transplants from localities where it is already present.

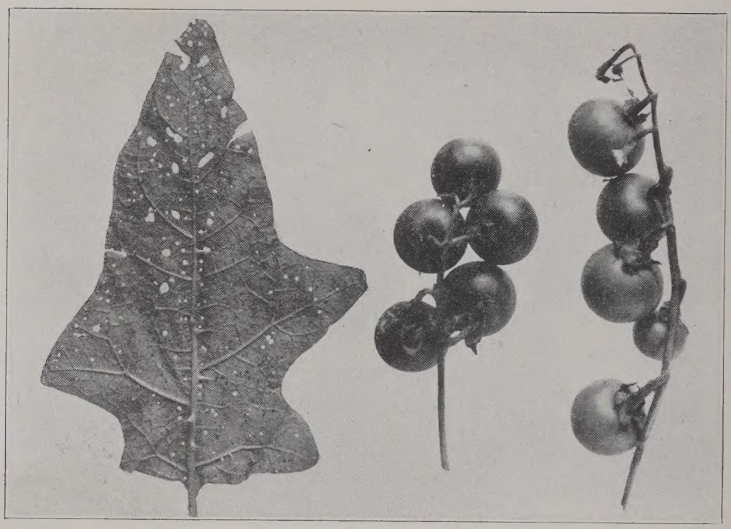

Fig. 13. Leaf and fruit characters of horse nettle, a common perennial weed which carries mosaic over winter. Note the characteristic spines on the leaf. The holes are due to flea-beetle injury.

MOSAIC ON HORSE NETTLE AND CLAMMY GROUND CHERRY

Mention has already been made of the fact that the horse nettle (Fig. 13) and clammy ground cherry (Fig. 12) may also harbor mosaic.

Mosaic in a conspicuous form was found in abundance on both of these weeds in a peach orchard near Vincennes, June 28, 1921. A clump of clammy ground cherries showing mosaic was found on July 27 along the edge of a field near LaFayette in which tomato mosaic had occurred the previous year. Mosaic was noted on horse nettle near a canning factory at Indianapolis on September 7.

Among the 81 tomato fields visited in the survey described above, clammy ground cherry was noted in seven fields and horse nettle in thirteen. In three fields, all in Marion county, mosaic was noted on clammy ground cherry and also occurred on the tomatoes. Mosaic was noted on horse nettle in only one field, a garden near Kokomo in which mosaic also occurred on smooth ground cherry and on the tomatoes.

As carriers of mosaic, these weeds are not as important as the species previously discussed because they are not as abundant in the tomato regions. Nevertheless these weeds should be recognized as enemies of the crop where they occur.

MOSAIC CONTROL SUGGESTIONS

Transplants from greenhouses and plant-beds in which tomato mosaic is present should not be used.

If such plants are used, all mosaic plants detected should be rogued out before pulling the plants. Frequent washing of the hands with soap and

water will minimize the danger of spreading mosaic during the transplanting operation.

Tomato growers and tobacco growers as well should recognize in the perennial ground cherries and horse nettle a distinct danger to their crop.

Drastic measures should be taken to eradicate these weeds in and near seedbeds, plant-beds, and greenhouses to be used for tomatoes. A zone 200 to 400 feet wide should be kept free of these weeds.

Furthermore, during the early part of the season, these weeds should be destroyed or at least kept down in and around the tomato field by frequent cultivation and hoeing. A zone 100 to 200 feet wide around the edge of the field should be included in this campaign. When the rootstocks are not destroyed, new shoots reappear promptly and frequent attention to their destruction is essential.

Other related perennials such as bittersweet and matrimony vine and related annual weeds such as nightshade, Jimson weed, and certain ground cherries should be destroyed in and near plant-beds and tomato fields.

Greenhouses to be used for tomatoes should be kept free of volunteer tobacco and tomato plants, petunias, and all of the related weeds and ornamentals.

Plant-beds should be kept clear of all weeds and remnant tomato plants during the summer and should not be used for peppers or eggplants.

It is advisable not to grow potatoes near tomato fields.

If mosaic is detected in the field on a few tomato plants early in the season, these should be destroyed since they may otherwise serve as centers of infection. This is also important in the greenhouse crop just before the pruning operation.

Control of the insect carriers such as plant lice and flea-beetles is advisable in greenhouses and plant-beds and, if feasible, in the field during the early part of the season. Greenhouses may be fumigated with nicotine or hydrocyanic acid. A Bordeaux spray with nicotine sulphate and an arsenical added may be used in the plant-bed and the field.

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